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Research article

(Sub-)Antarctic endemic cyanobacteria from benthic mats are rare and have restricted geographic distributions

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The Antarctic terrestrial macrobiota are highly endemic and biogeographically structured, but whether this also holds true for microbial groups remains poorly understood. We studied the biogeographic patterns of Antarctic cyanobacteria from benthic microbial mats sampled in 84 lakes from two sub-Antarctic islands, as well as from eight Antarctic Conservation Biogeographic Regions (ACBRs) which were previously defined based mainly on macroscopic taxa. Analysis of 16S rRNA gene sequences revealed that Antarctic and sub-Antarctic lakes host significantly different cyanobacterial communities, yet that the bioregionalization pattern did not correspond to the division into ACBRs. Both Antarctic and sub-Antarctic lakes contain a high number of potentially endemic taxa (41% of the total diversity), of which 33.3% attain a relative abundance of < 1%. Our findings highlight the uniqueness of Antarctic microbiota and the need for increased protection of inland waters in both Antarctica and the sub-Antarctic islands.

Keywords: ACBRs, Antarctica, benthic mats, biogeography, cyanobacteria, lakes, sub-Antarctic islands

Introduction

Antarctic terrestrial macrobiota shows high levels of endemism (De Smet and Gibson 2007, Pugh and Convey 2008, McGaughran et al. 2010, Collins et al. 2023), which has been attributed to their long-term survival in ice-free refugia during glacial maxima and the long-term geographic isolation of the continent (Convey and Stevens 2007, Fraser et al 2014). Continental-scale analyses of various taxonomic groups (Terauds et al. 2012, Dartnall 2017) revealed that the Antarctic terrestrial macrobiota are also biogeographically structured, which has prompted the delineation of 16 Antarctic Conservation and Biogeographic Regions (ACBRs) within the Continental

and Maritime Antarctica (Terauds and Lee 2016). The ACBR framework is now considered an integral part of Antarctic science, policy and management, and is frequently used as the null hypothesis in Antarctic biodiversity studies (Chown et al. 2015, Convey and Peck 2019, Hughes et al. 2019, Colesie et al. 2023).

For the microorganisms studied so-far in Antarctic lakes and soils, results are not consistent between different taxonomic groups. Indeed, lake diatoms at the morphospecies level adhere to this ACBR scheme (Verleyen et al. 2021), while this biogeographic subdivision of the Antarctic does not fully reflect soil bacterial distribution (Varliero et al. 2024). The incidence of endemism might also differ between different taxonomic groups as shown in a recent large-scale comparison of microbiome composition of polar lakes (Tytgat et al. 2023). This bipolar comparison revealed that the number of sequences being unique to the Antarctic differed between bacteria and microeukaryotes, but also between different phyla in both domains of life. This potential difference in the incidence of endemism and degree of biogeographic structuring between taxa might be partly related to taxon-specific differences in dispersal capacities and e.g. the ability to produce resting stages, go into dormancy and/or to survive wind-mediated dispersal (Tytgat et al. 2023). However, while this bipolar comparison of microbiome composition underscored the unique characteristics of Antarctic microbial communities, the geographic distribution of the sequence data in Tytgat et al. (2023) was not compared with that of related sequences stored in public databases and obtained from (sub-)tropical and temperate regions. This evidently prevents to assess whether the lineages are truly endemic to the Antarctic or, alternatively, have a wider geographic distribution. These comparisons exist only for a few microbial groups, including coccal green algae (De Wever et al. 2009) a terrestrial diatom species complex (Pinseel et al. 2020), and these indeed revealed the presence of distinct lineages or species that are restricted to the Antarctic. Albeit in these comparisons, the geographic coverage and extent of the reference database used evidently influences the assessment of whether taxa appear endemic or not, these DNA-based findings were congruent with a recent study in diatoms which revealed that 44% of the morphospecies are restricted to the Antarctic (Verleyen et al. 2021). For other microbial groups, such region-wide taxonomic inventories using a sufficient amount of samples are, however, still lacking, which prevents to assess their degree of endemism and whether their biogeographies adhere to the ACBR scheme.

A conspicuous feature of many Antarctic lakes is that primary production is largely limited to benthic microbial mats (Vincent 2000a), which are dominated by filamentous cyanobacteria such as *Leptolyngbya* spp., *Oscillatoria* spp., *Phormidium* spp. and *Phormidesmis* spp. (Taton et al. 2003, Komarek et al. 2008, Vincent and Quesada 2012, Pessi et al. 2018, 2023). Some cyanobacterial taxa/OTU appear to be endemic to Antarctica (Jungblut et al. 2010, Komarek et al. 2012, Kleinteich et al. 2017) and novel taxa have yet to be discovered, as recently revealed by Pessi et al. (2023) using a metagenomics approach. Other cyanobacterial lineages from Antarctic lakes have been observed in the Arctic or other cold habitats such as alpine lakes, whereas others have a cosmopolitan distribution (e.g. they were reported from polar, temperate and tropical regions; Kleinteich et al. 2017, Pessi et al. 2018, 2023).

Only a few studies have compared the obtained sequences with all data present in public databases (i.e. GenBank) to determine their degree of endemism (Pessi et al. 2018). Information on the biodiversity and incidence of endemism for lacustrine microorganisms is crucial for developing urgently-needed and science-based conservation strategies for Antarctic habitats in ice-free regions, which is needed for inland lakes (Hawes et al. 2023) and edaphic ecosystems (Lebre et al. 2023).

Here, we aimed to provide a more complete picture of the diversity and community structure of benthic lacustrine cyanobacteria based on the analysis of 84 lakes' samples collected across the Continental and Maritime Antarctic regions in eight ACBRs, and in two sub-Antarctic islands. We specifically tested whether the distribution of cyanobacteria is congruent with the ACBRs framework (Fig. 1). We hypothesize 1) that cyanobacterial communities differ between Antarctic (i.e. Continental and Maritime Antarctica) and the sub-Antarctic lakes due to their contrasting environmental characteristics and geographic isolation yet that their biogeographic structuring is incongruent with the ACBRs scheme, in contrast to other life forms that are probably more dispersal-limited (e.g. macrobiota and diatoms; Convey et al. 2014, Schulte et al. 2022); and 2) that the degree of endemicity is higher in the Antarctic lakes compared to those in the sub-Antarctic because long-distance dispersal in the latter region is aided by the Southern Hemisphere westerly winds as shown for moss, liverwort, lichen and pteridophyte floras (Muñoz et al. 2004).

Material and methods

Sampling and measurements

Eighty-nine microbial mats were collected from 84 lakes or ponds across eight ACBRs from Antarctica (n = 75), and the sub-Antarctic Macquarie (n = 6) and Marion (n = 8) Islands from the Southern Ocean (Fig. 1A). Antarctica is classically divided into two zones with a different climate and separated by the Gressitt Line, namely the Maritime Antarctic (Peninsula) and the Continental Antarctic (Chown and Convey 2007). Our dataset covers two and six ACBRs, in the Maritime and Continental Antarctic, respectively. A detailed description of all the sampled sites can be found in the Supporting information.

The mats were sampled during the period 1993–2013 during field expeditions of national and international research programs following a standardized protocol (Sabbe et al. 2004). Visible microbial mats were collected from the littoral zone (~ 20–50 cm depth) using a sterilized spatula. All

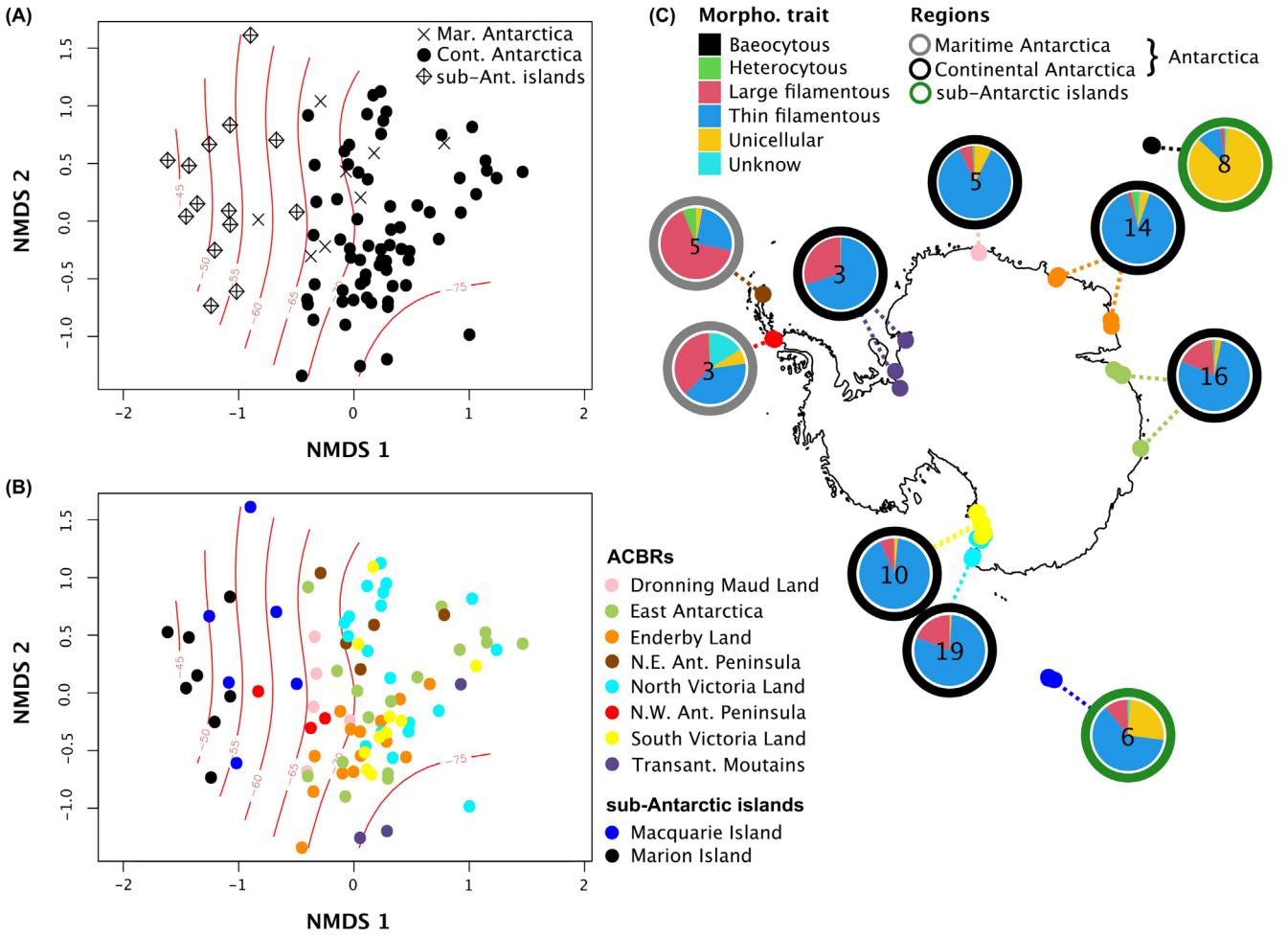

Figure 1. (A) metaMDS on the Bray–Curtis similarity matrix based on Hellinger transformed abundance data based on OTUs. Shapes represent the three main regions: Maritime Antarctica, Continental Antarctica and sub-Antarctic islands . Red curves represent the *ordisurf* function (R package 'vegan') fitting of generalized additive model (GAM) of latitude on the metaMDS ordination. (B) metaMDS as in (A). Colors represent the different ACBRs or sub-Antarctic regions investigated. (C) Map showing the sampling locations. The pie charts present the relative abundance of the different morphological types in each ACBRs. The numbers at the center of the pie charts represent the number of investigated samples in this study for each region.

samples were immediately stored at −20°C and kept frozen upon DNA extraction. Measurements of conductivity and pH were conducted on 79 and 71 samples, respectively, as described in Pessi et al. (2018).

DNA extraction, PCR and sequencing

Partial 16S rRNA sequences were obtained as described by Pessi et al. (2016). DNA was extracted using the PowerSoil DNA Isolation kit (MOBIO). The V3–V4 region was targeted by PCR using cyanobacteria-specific primers CYA359F and CYA781Ra/CYA781Rb (Nübel et al. 1997). PCR mixture consisted of 1× PCR buffer with 1.5 mM $MgCl_2$, 1 mg ml^{-1} BSA, 200 µM of each dNTP, 0.2 µM of each primer, 1 U SUPER TAQ plus DNA polymerase (HT Biotechnology), and 4 ng $µl^{-1}$ template DNA in a final volume of 50 µl. PCR amplification was carried out with an initial denaturation step at 94°C for 5 min, followed by 34 cycles of 94°C for 1 min, 57°C for 1 min and 68°C for 1 min, and a final elongation at 68°C for 5 min. For five randomly chosen samples, PCR duplicates were made to validate the robustness of the workflow. For each sample, three independent PCR reactions were pooled, purified (GeneJet PCR Purification Kit, ThermoScientific) and quantified (Quant-iT PicoGreen dsDNA Assay Kit, Life Technologies). Libraries were pooled in equimolar concentrations and sent to Genewiz (South Plainfield, NJ, USA) where ligation of sequencing adapters and sequencing was done using the Illumina MiSeq platform (Illumina) with 2 × 300 bp paired-end libraries.

Bioinformatic analysis to obtain quality filtered cyanobacterial OTUs

A read quality control and chimeric sequences filtering protocol based on UPARSE (Edgar 2013) was adapted from Pessi et al. (2016). The paired-end reads were merged and

filtered (–maxdiffs 10, –maxdiffpct 8), and reads that did not contain primer and barcodes in the 3' and 5' ends were removed. Two and zero mismatches were allowed for primer and barcode sequences, respectively. Reads with a maximum expected error of more than 0.5 and smaller than 370 bp were removed. After singleton removal, the remaining sequences were denoised to remove chimeras and sequencing errors using unoise3 (Edgar 2016). The resulting denoised zero-radius operational taxonomic units (ZOTUs) were then clustered into OTUs using a 99% similarity threshold (Edgar 2013). The most abundant sequence in each OTU cluster was selected as the representative sequence. OTUs with < 10 reads in the whole OTU table were finally removed.

After occurrence inspection of the PCR duplicate samples (Supporting information), mock communities and PCR duplicate samples were removed from the OTU table and only one sample with the highest read number was kept among PCR duplicate of the same sample.

Taxonomic affiliation and geographic distribution of OTUs

OTUs were first classified with the RDP classifier (Wang et al. 2007) implemented in QIIME pipeline (Caporaso et al. 2010). The taxonomic classification of cyanobacterial OTUs was subsequently refined by comparison with sequences from the GenBank nucleotide (nt) collection (accessed 9 April 2024). For this, closely related sequences (≥ 94.5% similarity, corresponding to the genus taxonomic rank according to Yarza et al. 2014) were retrieved using BLAST 2.8.1+ (Boratyn et al. 2013). The sequences with the highest similarity to each OTU were manually selected. To address the taxonomy of 'uncultured bacterium' or 'uncultured cyanobacterium', as well as to remove potential chimeras, a phylogenetic tree was built using RaxML ver. 8 (Stamatakis 2014) including the cyanobacterial OTUs, their close relative sequences taken from NCBI (nt) database and the CyanoSeq database (Lefler et al. 2023), which consist of (near) full length 16S rRNA gene sequences with curated taxonomy (Supporting information). Based on their taxonomy (Komarek et al. 2014) and phylogenetic position, a morphologic trait was subsequently assigned to each OTU: 'unicellular', 'thin filamentous', 'large filamentous', 'heterocytous' and 'unknown' (i.e. in the case of sequences with taxonomy above family rank, for which the morphological trait could not be assigned).

The geographic distribution of the OTUs was inferred based on the distribution of similar sequences (≥ 99% similarity) from GenBank. They were categorized as follows: 'endemic' (i.e. OTUs sharing less than 99% of similarity with any other published sequences or sharing at least 99% of similarity with sequences only reported from the southern polar region); 'polar' (i.e. OTUs sharing more than 99% of similarity with sequences from the Arctic and the Antarctic), 'alpine' (i.e. OTUs sharing more than 99% of similarity with sequences from polar and high altitude regions) and 'cosmopolitan' (i.e. OTUs sharing more than 99% of similarity with at least one sequence from non-polar and non-alpine regions) (Supporting information). These definitions are dependent of the geographic coverage of the public databases and the genetic marker used, knowing that only the cosmopolitan distribution can certainly be proven.

In order to examine the most abundant and the rarest OTUs fraction of Antarctica (i.e. Continental and Maritime Antarctica) and sub-Antarctic islands, OTUs encompassing > 90% of the total OTU counts were considered as the 'abundant fraction' whilst those encompassing < 1% of the total OTU counts were considered as the 'rare fraction'.

Analysis of cyanobacterial community structure

Beta diversity analyses were performed using R ver. 4.1.0 (www.r-project.org). Normal distribution and homoscedasticity of pH and conductivity values were tested through the Shapiro–Wilks test and the Bartlett's test using the package 'stats' (ver. 4.1.0), whilst skewness and kurtosis were investigated with the package 'moments' (ver. 0.14.1; Komsta and Novomestky 2015). For conductivity, the dataset was $\log(x+1)$ transformed in order to attenuate skewness. Finally, the OTU abundance table was Hellinger transformed prior to multivariate analysis to minimize the effect of differences in library size (Legendre et al. 2005, Peres-Neto et al. 2006).

To visualize community structure relationships, the Hellinger transformed abundance OTU table was converted into a dissimilarity matrix using Bray–Curtis similarities and a nonmetric multidimensional scaling (NMDS) ordination was done using the *metaMDS* function ('vegan' package, ver. 2.5-7; Oksanen et al. 2019). Then, the *ordisurf* function ('vegan' package) was used to fit the latitude on the ordination in order to determine its correlation (Wood 2003, Marra and Wood 2011). The *ordisurf* function uses a generalized additive model (GAM) to model the latitude on the metaMDS ordination, with the function *gam* ('mgcv' package, ver. 1.8-35; Wood et al. 2016). To test for significant differences between the communities, PERMANOVA was implemented using the *pairwise.adonis* function ('pairwiseAdonis' package, ver. 0.4; Martinez Arbizu 2020).

The effect of spatial parameters on cyanobacterial community structure was analysed using principal coordinates of neighborhood matrix (PCNMs; Borcard and Legendre 2002) as described by Sakaeva et al. (2016). The latitude and longitude of each sample were first used to calculate a geographic distance matrix using the function *distGeo* of the command *distm* ('geosphere' package ver. 1.5-14; Hijmans 2014). This matrix was used to calculate PCNM eigenvectors using the function *pcnm* ('vegan' package) with the smallest PCNM (PCNM1) representing large spatial scales and the biggest ones (PCNM*) fine spatial scales.

To explain variations in community structure, we performed redundancy analysis (RDA). The variation partitioning (Borcard et al. 1992, Peres-Neto et al. 2006) was used to determine the relative importance of geographic distance (spatial gradient), conductivity and pH on cyanobacterial

community structure as in Sokol et al. (2013). First, a distance-based redundancy analysis (dbRDA; McArdle and Anderson, 2001) was used to model variation in community structures as a function of either environmental (pH and conductivity) or spatial (PCNMs) variables. Forward stepwise model selection (Blanchet et al. 2008) based on adjusted R^2 (Beisner et al. 2006, Peres-Neto et al. 2006, Nabout et al. 2009, Legendre and Legendre 2012) was used to select PNCMs that best explained variation in community structures. Then, the PCNMs were combined with the environmental variables into a single dbRDA model to calculate the total variation in community structures, using the function *varpart* ('vegan' package). The adjusted R^2 values give us the among site variation in community structures explained by both environmental and spatial variables [E + S], by pure environmental [E | S], spatially structured by the environment [E ∩ S], pure spatial [S | E] or unexplained.

Results

Illumina sequencing resulted in 3 981 506 reads of which 90.5% was retained after quality filtering. After further processing (dereplication, removal of singletons, chimeric and non-cyanobacterial reads, and removal of OTUs with < 10 reads per sample), 310 cyanobacterial OTUs (99% similarity) representing 45.3% of the original bacterial reads were kept. Of the 310 OTUs, 146 OTUs (47.1%) were detected in both Antarctica (which includes both Continental and Maritime Antarctica) and the sub-Antarctic islands, 133 OTUs (42.9%) were restricted to Antarctica and 31 OTUs (10%) were detected only in the sub-Antarctic islands (Supporting information).

Cyanobacteria differ between Antarctica and the sub-Antarctic islands, but not between ACBRs

The cyanobacterial communities differed between Antarctica and the sub-Antarctic islands as shown by the NMDS analysis (Fig. 1A), of which the first axis is correlated with latitude (Pearson correlation with NMDS1: $R^2 = 0.78$, $p < 0.01$). These differences were confirmed by PERMANOVA, which showed that the sub-Antarctic communities differed significantly from those in Continental Antarctica (pairwise.adonis: $r^2 = 0.081$, adjusted p-value = 0.003) and in Maritime Antarctica (pairwise.adonis: $r^2 = 0.120$, adjusted p-value = 0.006) (Supporting information). Continental and Maritime Antarctic communities were also significantly different (pairwise.adonis: $r^2 = 0.0342$, adjusted p-value = 0.018), yet the bioregionalization pattern within Antarctica did not mirror the ACBR framework (Fig. 1B). Variation partitioning revealed that 14.8% of cyanobacterial community structure was explained by spatial parameters and only 4.9% by environmental factors (pH and conductivity) (Supporting information). The significant spatial parameters were PCNMs reflecting large scale geographical distances (i.e. between Antarctica and the sub-Antarctic Islands). In addition, variation partitioning analysis showed that latitude was included in the PCNMs component (Fig. 2).

The dominant genera also differed between Antarctica and the sub-Antarctic islands as revealed by the taxonomic assignment of OTUs morphotypes (Fig. 1C, Supporting information). Sequences related to thin filamentous cyanobacteria of the genera *Leptolyngbya* (32% of the reads) and *Phormidesmis* (23.8%) were dominant in Continental Antarctica, while sequences related to large filamentous cyanobacteria of the genera *Phormidium* (6.1%) were more abundant in Maritime Antarctica. By contrast, sequences related to unicellular cyanobacteria of the genera *Cyanobium* (28.7%) and *Synechococcus* (16.4%) dominated the communities in the sub-Antarctic islands, and particularly Marion Island.

The distribution patterns and taxonomic composition differ between the abundant and rare fractions

The taxonomic composition of the rare fraction (< 1% relative abundance) was markedly different from that of the abundant fraction (> 90% relative abundance; Fig. 3A, Supporting information), as the rare fraction encompassed a higher number of heterocystous and unicellular morphotypes than the abundant fraction. The latter fraction in the Antarctic lakes was characterized by filamentous genera such as *Leptolyngbya* (34.3% of the number of reads), *Phormidesmis* (24.7%), *Stenomitos* (8.6%) and *Phormidium* (5.9%), whilst it was the unicellular *Cyanobium* (28.7%), the filamentous *Phormidesmis* (24.5%) and the unicellular *Synechococcus* (15.6%) for the sub-Antarctic lakes.

With no clear differences between ACBRs (Supporting information), around 46% of the OTUs present in the Antarctic and sub-Antarctic lakes were cosmopolitan, whilst

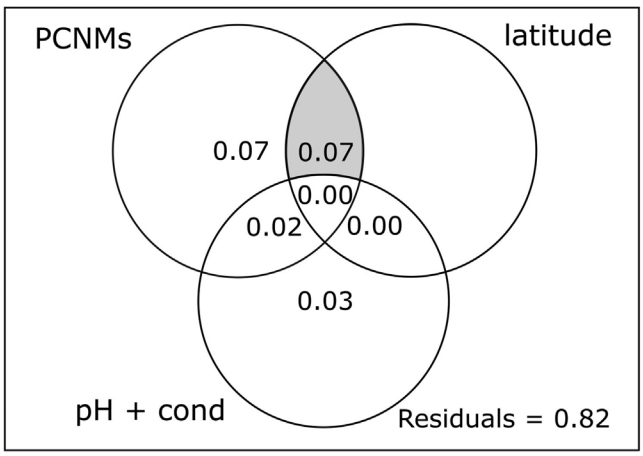

Figure 2. Addition of latitude in the variation partitioning revealing its correlation with spatial parameter (in grey: 7% on the 14% of PCNMs). PCNMs (principal coordinate of neigborhood matrix) are eigenvectors ranged from large spatial scales (PCNM1) to fine spatial scale (PCNM*). Variation partitioning was calculated in R studio using function *varpart* ('vegan' package, ver. 2.5-7; Oksanen et al. 2019).

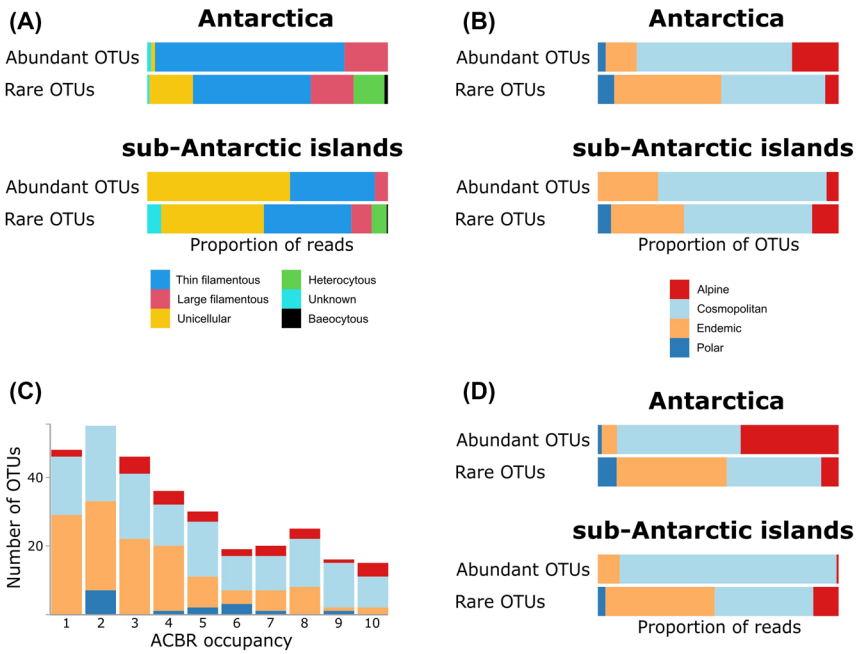

Figure 3. Comparison of the 75 Antarctic and 14 sub-Antarctic cyanobacterial communities. (A) The relative abundance of the different morphotypes of 'abundant' OTUs (i.e. OTUs encompassing > 90% of the total OTU counts) and the 'rare fraction' (i.e. those encompassing < 1% of the total OUT counts) in Antarctic (upper panel) and sub-Antarctic lakes (lower panel). Colors represent the OTU morphotypes. 'Unknown' morphotype corresponds to OTUs whose taxonomic rank identification was too high (e.g. family) to discriminate between one or another morphological trait. (B) The proportion of 'endemic', 'alpine', 'polar' and 'cosmopolitan' OTUs (expressed as number of OTUs) in the 'abundant' and 'rare' fraction of Antarctic and sub-Antarctic lakes. (C) The number of 'endemic', 'alpine', 'polar' and 'cosmopolitan' OTUs occurring in 1, 2, ...10 ACBRs (i.e. the occupancy). (D) The proportion of 'endemic', 'alpine', 'polar' and 'cosmopolitan' OTUs (expressed as number of reads) in the 'abundant' and 'rare' fraction. The color code in (B)–(D) represents the geographic distribution of the OTUs.

41% were considered as endemic, as revealed by the manually curated blastn search performed in NCBI nucleotide (nt) database. This analysis allowed to retrieve the original information of each publicly available sequence with which our OTUs shared above 99% of similarity. Although the method is limited by the geographic coverage of the database and the genetic marker used, we considered an OTU as potentially 'endemic' if they shared less than 99% of similarity with any other sequences or if it shared more than 99% of similarity with sequences which were previously only detected in the Antarctic. In this way, we observed that the geographic distribution of sequences belonging to the rare fraction was markedly different from that of members from the abundant fraction (Fig. 3B, Supporting information).

Endemic OTUs were more prevalent within the rare fraction whereas the abundant fraction consisted mostly of cosmopolitan OTUs. This difference was particularly prominent in the Antarctic lakes. The abundant fraction of the Antarctic lakes was represented by taxa with a cosmopolitan distribution (64.5% of the number of OTUs), followed by sequences with an alpine (19.4%), endemic (12.9%) and polar (3.2%) distribution. The abundant fraction of the sub-Antarctic lakes was characterized by an even higher proportion of taxa with a cosmopolitan distribution (70%), followed by those with an endemic (25%) and alpine (5%) distribution. By contrast, the rare fraction in Antarctic lakes was characterized by OTUs with an endemic distribution (44.4% of the OTUs), followed by cosmopolitan (43.2%), polar (6.8%) and alpine (5.6%) distributions. The rare fraction in the sub-Antarctic islands encompassed a higher proportion of OTUs with a cosmopolitan distribution (53.2%), followed by those with an endemic (30.3%), alpine (11%) and polar (5.5%) distribution. Interestingly, when considering the relative abundances of the sequences instead of the number of OTUs (Fig. 3D, Supporting information), up to half of the abundant fraction in the Antarctic lakes is characterized by OTUs with a cold distribution (alpine: 40.7%; endemic: 6.3%; polar: 1.6%) whilst the vast majority of the sequences in the abundant fraction in the sub-Antarctic lakes consist of cosmopolitan taxa (90.1%). Finally, the analysis of ACBRs and sub-Antarctic islands occupancy showed that endemic OTUs are mostly restricted to a few ACBRs or islands, compared to cosmopolitan ones that are widespread across Antarctica (Fig. 3C).

Discussion

Cyanobacterial communities differ between Antarctica and the sub-Antarctic islands

Our analyses revealed significant differences in cyanobacterial community composition and structure between Antarctic

and sub-Antarctic lakes. These marked differences were also observed in other taxonomic groups such as terrestrial nematodes, mites and springtails (Chown and Convey 2007), as well as in aquatic invertebrates (Dartnall 2017) and other freshwater (Verleyen et al. 2021, Tytgat et al. 2023) and edaphic microorganisms (Lebre et al. 2023, Varliero et al. 2024). Our results also showed that the taxonomic composition, corresponding to specific morphological traits of the cyanobacteria in these mats, is different between Antarctica and the sub-Antarctic islands. Thin (1–3 μm) filamentous taxa (e.g. *Leptolyngbya*, *Phormidesmis*) followed by larger filamentous taxa (e.g. *Phormidium*, *Microcoleus*) dominated Antarctic lakes, whilst unicellular taxa (e.g. *Chamaesiphon*, *Cyanobium* and *Synechococcus*) dominated the sub-Antarctic lakes in Marion Island and were also particularly abundant, although not dominant, in the sub-Antarctic lakes in Macquarie Island. These findings agree with previous observations which reveal that cyanobacterial taxa dominate benthic mats, with filamentous taxa (e.g. *Leptolynbya, Phormidium* and *Stenomitos*) particularly prominent in Antarctic lakes (Vincent 2000b, Taton et al. 2006, Fernandez-Carazo et al. 2011, Sumner et al. 2016, Jungblut and Vincent 2017, Pessi et al. 2018, 2023, Jackson et al. 2021). The high cyanobacterial abundance in benthic mats has been attributed to the general lack of large metazoan grazers (e.g. crustaceans) compared with lower latitude lakes (Zawierucha et al. 2019, Tytgat et al. 2023 and references therein). This lack of top–down control by grazers results in low levels of bioturbation of sediments and biofilms (Jungblut et al. 2012) in Antarctic lakes promoting the formation of perennial microbial mats, which are physically structured by filamentous cyanobacteria and micro-algae (Tytgat et al. 2023). A higher proportion of unicellular OTUs in the sub-Antarctic islands compared to the Antarctic lakes was also encountered by Tytgat et al. (2023) and may be due to the higher planktonic primary production and/or the higher bioturbation and grazing by larger metazoan invertebrates in the sub-Antarctic islands compared to Antarctica. The higher planktonic primary production in the sub-Antarctic lakes is the result of the complete mixing of their water columns due to the lack of seasonal lake ice cover and high wind speeds, which keep non-motile planktonic taxa in suspension (Vincent and Laybourn-Parry 2008). Moreover, in sub-Antarctic lakes, mosses and sometimes macrophytes cover the bottom of lakes and fill the niche occupied by the benthic cyanobacteria in Antarctic lakes (Smith and Ashton 1971, Douce et al. 2023). Velázquez et al. (2017) also found differences in the cyanobacterial composition during ice-covered versus ice-free periods of lakes in Byers Peninsula, with unicellular taxa (e.g. *Synechococcus* spp.) occurring especially during the ice-free season.

Cyanobacterial communities are not clearly differentiated among ACBRs

No clear difference in cyanobacterial community structure was observed between the ACBRs. However, the communities were significantly different, albeit with a relatively high p-value, between the Maritime Antarctic and Continental Antarctica. This marginally significant difference might be related to the sampling effort, which was lower in Maritime Antarctica, hindering to reveal a more significant difference in community structure compared to Continental Antarctica. The absence of differences in cyanobacterial community structure among the ACBRs is in agreement with a biogeographic survey of soil bacteria which revealed clear differences between Antarctica and the sub-Antarctic islands, but not between the ACBRs, and some difference but also overlap between Maritime and Continental Antarctica (Varliero et al. 2024). By contrast, the distribution of lake diatom species is congruent with the ACBR scheme (Verleyen et al. 2021). This difference can be in part attributed to differences in dispersal ability and life cycle characteristics between different freshwater taxa. Cyanobacteria are able to survive desiccation and other extreme conditions (Sakamoto et al. 2009) experienced during wind-mediated dispersal, compared to, for example, lake diatoms (Souffreau et al. 2010). It has been shown that some Antarctic cyanobacteria have an 'escape mechanism' from the lakes, as they form so-called 'lift-off' mats (Dudeja et al. 2010), allowing benthic cyanobacteria to move from the bottom of the lake to the surface and afterwards disperse to other terrestrial and aquatic environments (Wharton et al. 1983, Tanabe and Kudoh 2012). This might facilitate the colonization of different regions within the Antarctic continent (Herbold et al. 2014, Chown et al. 2015) and hence explain the lack of a clear structuring into the ACBRs. This efficient dispersal mechanism combined with a high resistance to the harsh conditions can also explain why quite a large number of the OTUs occur in all or nearly all ACBRs. Interestingly, the majority of the OTUs occurring in less than five ACBRs or sub-Antarctic islands are mostly endemic whilst those occurring between 5 and 10 ACBRs or sub-Antarctic islands were mainly cosmopolitan taxa. One scenario could be that these cosmopolitan taxa have colonized a lake system after its formation due to glacial retreat or isostatic uplift (Verleyen et al. 2012). These colonizing taxa might also be well-adapted for dispersal within Antarctica, leading to a quick spread between the different ACBRs and not leaving any footprint of biogeographical zonation at the 16S rRNA level considered in the present study.

High incidence of endemism in Antarctic cyanobacteria, yet endemic taxa are rare and have restricted distributions

A total of 40.6% of all OTUs appear endemic to Antarctica or the sub-Antarctic islands. This level of endemism is comparable with lacustrine diatoms in both regions (Verleyen et al. 2021), and with lichens in Antarctica (33–50%; Peat et al. 2006). It is however clearly lower than the incidence of endemism found in Antarctic springtails (90%; Baird et al. 2019), bdelloid rotifers (95% endemics in Antarctica; Iakovenko et al. 2015) and tardigrades (73%; Guidetti et al. 2019). The degree of endemism in cyanobacteria mightbe an underestimation because 16S rRNA gene might not be

variable enough and the used amplicon too short to delineate taxa at the species level (Cho and Tiedje 2000), despite the fact that Taton et al. (2003) tested that the 16s rRNA V3-V4 region was representative of the complete sequence for cyanobacteria. On the other hand, this assessment of the endemism degree might also be an overestimation as the public database used to assess the geographic distribution of OTUs might not be complete. We are aware that our careful selection and characterization of OTUs (e.g. chimeric removing, removing OTUs ≤ 10 reads, blastn approach) might not fully solve these problems. However, despite these potential limits, our study showed that the endemic cyanobacteria only accounted for 9.4% of the total read counts. Moreover, while the most abundant OTUs were generally cosmopolitan, 68% of the endemic OTUs were rare in Antarctica and 56% in the sub-Antarctic islands. This has evidently important consequences for the conservation of these biota in the face of climate change and increased human impacts (Chown et al. 2015) as rare taxa are evidently more difficult to protect than those with larger population sizes which are less prone to extinction (Hughes et al. 2015, Wauchope et al. 2019). However, protecting the rare biosphere is crucial, because those taxa may have important ecological roles, and serve as a large reservoir of genetic and functional diversity which may provide resilience to change (Lynch and Neufeld 2015).

What also became evident from this study is that the abundant and widespread OTUs in the sub-Antarctic islands had a cosmopolitan distribution, whereas in Antarctica, relatively more OTUs were restricted to cold environments (i.e. cold-ecotypes: endemic, polar or alpine distribution). Moreover, the three most abundant OTUs in Antarctica had an alpine distribution. This is in line with previous observations about cold-habitat-specific cyanobacterial assemblages dominating Antarctica and often absent in other climatic zones (Jungblut et al. 2010, Kleinteich et al. 2017), which could be explained by a higher ecological success of taxa adapted to general cold and extreme conditions typical of Antarctic, Arctic and alpine environments (Hessen 2007).

Moreover, in both sub-Antarctic and Antarctic lakes, the abundant fraction was characterized by only a few but widespread and cosmopolitan OTUs, while the rare fraction encompassed mainly endemic OTUs with a limited range size. A possible explanation is that large population sizes may increase the probability of dispersal (Nemergut et al. 2011) and that some cyanobacterial taxa may be better adapted for dispersal via, e.g. aeolian transport (Herbold et al. 2014) than others. Alternatively, but data to fully test this is lacking, the rare and endemic OTUs might be the result of recent speciation events (Tytgat et al. 2023) and the time since speciation might have been too short for widespread dispersal within the Antarctic in contrast to the cosmopolitan taxa. In turn, this, as well as differences in dispersal capacities, could explain the higher proportion of cosmopolitan taxa being present in several ACBRs compared to the endemic OTUs being restricted to a few ACBRs. As already discussed, the cosmopolitan OTUs might have high dispersal capacities which might have resulted in their widespread distribution in the Antarctic and the lack of clear biogeographic structuring. In a climate change scenario, these widespread and cosmopolitan taxa might therefore be more likely to colonize new habitats.

The need for protecting the sub-Antarctic islands

Microbial communities in sub-Antarctic islands are poorly studied and have only recently been included in biogeographic studies of lakes (Verleyen et al. 2021, Tytgatt et al. 2023) and soils (Lebre et al. 2023, Varliero et al. 2024). We encountered a relatively high degree of potential endemism in the sub-Antarctic lacustrine cyanobacterial communities, which has never been reported before. The incidence of endemism appeared to be lower in the sub-Antarctic islands than in the continent, possibly due to wind-driven dispersal between the islands and land masses at the temperate latitudes in the Southern Hemisphere was shown for cryptogamic floras (Muñoz et al. 2004). Tytgat et al. (2023) also revealed that a lower proportion of microorganisms was endemic in the sub-Antarctic lakes compared to the Antarctic systems. Similarly, the incidence of endemism in diatoms at the morphospecies level is also lower in sub-Antarctica compared with the Antarctic continent (Verleyen et al. 2021). Given that the incidence of endemism is relatively high (34%), even compared with the estimations of cyanobacteria endemicity to Antarctica (38%), our study further justifies the inclusion of the sub-Antarctic islands surrounding the Antarctic continent to the ACBRs rationale, as already proposed by Lebre et al. (2023). The natural barriers within the sub-Antarctic islands, between them and the rest of the World are being progressively degraded through human activities (Pertierra et al. 2017, Hughes et al. 2019). Therefore, conservation efforts should be enhanced to avoid human-induced introductions of non-native microbes in both Antarctica and the sub-Antarctic islands and homogenization of microbial floras between ice-free regions of the continent. Recommendations to minimize the human impact are given in the SCAR code of conduct for terrestrial research (Scientific Committee on Antarctic Research [SCAR] 2009, 2011).

Conclusions

In this study, we showed that the cyanobacterial community composition is different between Antarctic and sub-Antarctic lakes, but not among the ACBRs, which were generally delineated based on macroscopic organisms. We found a relatively high number of endemic taxa in both the Antarctic and the sub-Antarctic lakes, with a higher proportion in Antarctica. Also, a high amount of the encountered endemic taxa was rare, highlighting the urge for their protection. Finally, this study provides justifications to include the sub-Antarctic islands in the ACBRs rationale in order to improve the conservation measures of these regions.

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Author contributions

Benoit Durieu and **Valentina Savaglia** contributed equally to this publication. **Benoit Durieu:** Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Valentina Savaglia**: Data curation (supporting); Formal analysis (supporting); Methodology (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Yannick Lara**: Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (supporting). **Alexandre Lambion**: Investigation (lead); Writing – review and editing (supporting). **Igor S. Pessi**: Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Wim Vyverman**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Elie Verleyen**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Annick Wilmotte**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Resources (lead); Supervision (equal); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v41ns1s5b (Durieu et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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